IDENTIFYING FLORAL HOSTS OF CERAMBYCID BEETLES USING PALYNOLOGY

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Entomology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2017

Urbana, Illinois

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ABSTRACT

Pollen is an important food source for many insects including the adults of beetles whose larvae are important forest pests. I quantified the distribution of pollen-feeding in adults of several species of long-horned beetles (Coleoptera: Cerambycidae). Palynivory by cerambycid beetles is common in the subfamily Lepturinae and occurs sporadically in Cerambycinae. The current knowledge of feeding in this group is inferred from floral host records, which are biased against tall trees because they are inaccessible to naturalists. I present a simplified palynological method for extracting and quantifying pollen from the frass of 21 species of beetles collected on flowers, with pheromone-baited panel traps, and at lights. I identified pollen grains to genus or species when possible and estimated abundances using calculations based on standardized markers added to samples. I found a higher abundance of pollen grains in the frass of palynivorous beetles collected on flowers than in the frass of beetles collected otherwise. I used the Shannon-Wiener Index to describe the diversity of pollen in the frass of beetles collected from flowers. There was high alpha diversity of pollen grains in the frass of *Callimoxys sanguinicollis* (Olivier) on *Cornus drummondii* C.A.Mey. (Cornaceae) and *Molorchus bimaculatus* Say on *Cornus florida* L. Next, I described the pollen taxa in the frass of palynivorous beetles collecting in traps and at lights by calculating the mean abundance and proportions of pollen taxa. I found *Juglans nigra* L. (Juglandaceae), *Quercus* L. (Fagaceae), and *Vitis* L. (Vitaceae) in frass from *Anelaphus pumilus* (Newman). *Acer* L. (Sapindaceae), *Viburnum* L. (Caprifoliaceae), and *Quercus* was found in frass from *Cyrtophorus verrucosus* (Olivier). I recorded *Acer* and *Quercus* pollen in the frass of *Euderces pini* (Olivier). *Megacyllene caryae* (Gahan) frass contained *Quercus* and *Crataegus* Tourn. (Rosaceae) pollen. Finally, the abundance, richness, and composition of pollen grains in the frass of *Megacyllene caryae* varied with collection date (e.g., April 17 vs. April 25, 2016) and location (e.g., forest vs. urban sites). These results provide insight into the natural history and feeding behavior of long-horned beetles, potentially influencing conservation or pest management strategies for forest insects. Moreover, I provide a method to secure evidence of palynivory in insects without having to carry out dissections or field observations.

ACKNOWLEDGMENTS

I thank Steve Buck, Nathan Beccue, Jay Hayek, Derek Liebert, and the University of Illinois Committee on Natural Areas, the Champaign County Forest Preserves District, Vermilion County Conservation District, Natural Areas Committee of the Urbana Parks District, and the Illinois Department of Natural Resources for access to field sites. I appreciate funding support from The Alphawood Foundation of Chicago (to LMH). References samples were provided by the herbarium at the Illinois Natural History Survey and Feng Sheng Hu. Labor, data collection, and data processing provided by Michael P. Donovan, Thomas J. Sanchez, Suzanne Vachula, Natalie Diesel, Todd Johnson, Linnea Meier, Judy Mongold-Diers, and Christina Silliman are greatly appreciated. Sarah Lee aided in statistical analyses. Thanks to James B. Nardi for use of his microscope equipment. Pietra G. Mueller, Ingrid C. Romero, Derek S. Haselhorst, Jacklyn Rodriquez, Alejandra Restrepo, and Michael Urban provided expertise in pollen identification, microscopy, and palynology. To those who served on my Masters Committee: your time, effort, feedback, and encouragement was greatly appreciated. I also thank Kim Leigh, who always holds the Department of Entomology together. I thank my husband, David Aristizábal Urrea, who knows way too much about long-horned beetles for a social-cultural anthropologist. I thank my parents, Tavia S. Pigg and Wade N. Hazel, who encouraged me to appreciate the intrinsic value of nature during my youth at the Flying Pigg Farm and Butterfly Ranch in Reelsville, IN.

TABLE OF CONTENTS

INTRODUCTION

Beetles (Coleoptera) may be among the oldest lineage of pollinators (Lovell 1915, Labandeira et al. 2007). Many basal angiosperm taxa and gymnosperms are pollinated by beetles (Pellmyr et al. 1991, Kono and Tobe 2007, Thien et al. 2009, Peris et al. 2017). Pollen is a reward for beetle pollinators before the evolution of more specialized insect-pollinator relationships (Berhardt 2000, Friis et al. 2006). Although some species of beetles are critical for cross-pollination today, many others are considered "pollen predators" (Wäckers et al. 2007). The nutritional content of pollen varies across plant taxa (Liolios et al. 2016), but it likely provides palynivorous insects with essential nutrients such as protein, carbohydrates, lipids, vitamins, and minerals (Campos et al. 2008). Moreover, the acquisition of nutrients from pollen stimulates oogenesis in some sunflower weevils (Coleoptera: Curculionidae; Rana and Charlet 1997). Better establishing the pollen feeding behaviors of insect species will influence plant-insect relationships.

Pollen feeding by adult beetles could be explained by the nutrition acquired from larval feeding. Long-horned beetles ("cerambycids"; Coleoptera: Cerambycidae), for example, are woodboring as larvae and feed on hemicellulose, cellulose, and lignins (Filipiak and Weiner 2014). Adult feeding may satisfy dietary requirements when larvae feed on nutritionally poor plant tissues. Feeding on pollen as adults may therefore provide essential nutrients not acquired from a strict wood diet. For example, two introduced species of *Eucalyptus* L'Hér. (Myrtaceae) woodborers, *Phoracantha semipunctata* (F.) and *P. recurva* (Newman), in California demonstrated positive fitness when fed *Eucalyptus* pollen compared to other sources of nutrition, such as dog food, sucrose, and pollen grains from other regions in North America (Millar et al. 2003). Females that foraged on *Eucalyptus* pollen exhibited increased fecundity and produced larger clutch sizes than females fed other diets. Moreover, *Eucalyptus* pollen grains was detected in the frass of laboratory-reared (Hanks et al. 1993) and wild-caught (Hanks et al. 1998) *P. semipunctata*. In summary, feeding on suitable types of pollen affects the fitness of some adult long-horned beetles.

The main objective of the present study was to use palynological methods to assess the extent of palynivory in long-horned beetles and identify floral hosts by extracting and identifying pollen from their frass. Little is currently known about the feeding behavior of native cerambycid beetles in eastern North America. To achieve this objective, I first reviewed and summarized

floral host records in the literature. Next, I collected long-horned beetles on flowers and from pheromone-baited panel traps. I determined if beetles were palynivorous based on the abundance of pollen grains extracted from their frass. Pollen grains were identified to infer floral host associations of palynivorous beetles. I then compared pollen-feeding and associated floral hosts to those previously reported in the literature. Lastly, I assessed how the abundance, richness, and composition of pollen grains from the frass of *Megacyllene caryae* (Gahan) – a commonly collected beetle – was affected by the season and location of the beetle.

Long-horned beetles are economically and ecologically important. Most are woodborers during their larval stage and feed on the cambium, roots, or stems of trees, as well as healthy, stressed, dead, and decomposing wood (Linsley 1959, Hanks 1999). Lovell (1915) suggested that cerambycids are among the most abundant anthophilous insects in eastern North America, particularly those in the subfamily Lepturinae, known as "flower longhorns." Palynivory by adult cerambycids is common in many species in the Lepturinae and sporadic in Cerambycinae (Linsley 1959, 1963, 1964; Linsley and Chemsak 1976, Graham et al. 2012a). Several species of cerambycid beetles have been observed feeding on pollen or nectar on a variety of flowering plants in the region based on floral host records. The current knowledge of the feeding behavior and natural history of these organisms is restricted to anecdotal observations, primarily floral host records. I reviewed and summarized these records to describe patterns in floral hosts associations (Appendix A).

Recent advances in the chemical ecology of cerambycids have allowed more efficient collection methods. A broad range of beetles in large quantities can be collected using sex-aggregation pheromones (Hanks and Millar 2013, Millar and Hanks 2017) and panel traps (Graham et al. 2010, Allison et al. 2014). Sympatric and congeneric beetles usually share chemical motifs; however, species-specific minor components and host plant volatiles may inhibit attraction by congeneric species (Hanks and Millar 2013). Pheromonal parsimony enables the development of generic lures to attract a broad spectrum of cerambycid beetles (reviewed by Millar and Hanks 2017). In addition, sex-aggregation pheromones produced by cerambycines are well-documented. Synthesized pheromone lures can be used to monitor and characterize cerambycid communities in nature.

Palynology (pollen analysis) is a powerful tool for determining plant-pollinator or plant-palynivore relationships when direct observation of floral visits is not possible. Pollen grains can

be recovered from the insect cuticle and setae (Jones and Jones 2001, Jones 2012, Wappler et al. 2015), from the guts of palynivorous insects (Jones 2012), and the rectum of honey bees (Hymenoptera: Apidae: *Apis mellifera* L.; Dimou and Thrasyvoulou 2009). Previous investigations have also recovered pollen from beetle frass (Davidson and Evans 2010). Critical to the detailed palynological analysis of insect frass is the fact that the external morphology (e.g., ectexine) of pollen grains are taxonomically diagnostic (Faegri et al. 1989, Kapp 1969). In standard palynological sample processing, the cytoplasm of the pollen grain must be dissolved to allow identification (Faegri et al. 1989). Acetolysis, the controlled application of sulfuric acid, is used to accomplish this, which is as laborious as it is dangerous (Jones 2014).

The ectexine of the pollen grain is highly resistant to strong acids. Acetolysis leaves the ectexine, or outermost stratum of the pollen grain, intact (Jones 2014). The ectexine remains even as the cytoplasm is digested in the gut of palynivorous insects (Jones 2012). For this reason, the remains of pollen material can be easily identified in insect frass. In this paper, I introduce a simplified processing method for the extraction of pollen from frass. Because the cytoplasm of the pollen grain is digested in the gut, but the ectexine is excreted fully intact, my method does not require acetolysis and gut dissections. This, in combination with trapping facilitated by generic cerambycid pheromones, enabled us to provide direct evidence of pollen feeding in the species of cerambycid beetles that I captured.

MATERIALS AND METHODS

Study Sites

I collected cerambycid beetles in urban and forested sites in Champaign, Grundy, Piatt, and Vermillion Counties in Illinois, and Putnam County in Indiana (Table 1). Many of the larger study sites were primarily second-growth and old-growth hardwood forests dominated by oaks (Fagaceae: *Quercus* L.), hickories (Juglandaceae: *Carya* Nutt.), and maples (Sapindaceae: *Acer* L.) (Boggess 1964, Boggess and Bailey 1964, Edgington 1991, Shafer and Edgington 2003, Creutzburg 2004). The Illinois Forestry Plantation and South Arboretum sites comprise several species of trees that are non-native to east-central Illinois, such as *Larix* Mill. spp. (Pinaceae) and *Quercus robur* L. (Fagaceae; Mohlenbrock 1996).

Collecting Beetles

Beetles were collected from floral hosts previously reported in the literature (see Appendix A) and during their seasonal activity period in the study area (Hanks and Millar 2013, Hanks et al. 2014, Handley et al. 2015). Floral host information was recorded in the field. Individual beetles were removed from flowers and placed in 20-ml glass vials for at least 24 h to allow frass to accumulate.

Free-flying beetle specimens were collected from April to November, 2012 to 2016. I used black cross-vane panel traps (AlphaScents, Portland, OR) coated with the fluoropolymer dispersion Fluon® PTFE (AGC Chemicals Americas, Inc., Exton, PA) to improve trapping efficiency (Graham et al. 2010). Traps were modified to capture beetles alive by replacing trap basins with 2-l plastic jars that had the bottoms cut out and replaced with aluminum screen. Traps were hung ~0.5 m above the ground from inverted L-shaped frames constructed out of polyvinyl chloride irrigation pipe. Pheromone lures consisted of polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, 0.05 mm thick, Cousin Corp., Largo, FL) loaded with 50 mg of the racemic synthesized compounds (i.e., 25 mg of each enantiomer) in 1 ml of isopropanol. Pheromones were selected to target species of cerambycids, such as enantiomers of 2,3-hexanediol and 3-hydroxyhexan-2-ol for most cerambycines (see Hanks and Millar 2013, Millar and Hanks 2017) with minor components such as (*R*)-2-methyl-butanol-1-ol and 2-nonanone for *Phymatodes* Mulsant spp. and *Cyrtophorus verrucosus* (Olivier), respectively (Mitchell et al. 2015). Lures were replaced biweekly. Traps were serviced daily to minimize the

loss of frass produced by trapped beetles. *Anelaphus pumilus* (Newman) was collected using a 700-watt mercury vapor fluorescent lamp (General Electric, Fairfield, CT) suspended ~1.5 meters above the ground in front of a white sheet. As with the foraging beetles, individual free-flying beetles were placed in 20-ml glass vials for at least 24 h to allow frass to accumulate.

Taxonomic Assignments

Taxonomy of collected beetles follows Bezark and Monné (2013). Representative specimens of each species are available from the laboratory of LMH, and voucher specimens have been deposited in the collection of the Illinois Natural History Survey, Champaign, IL. Taxonomy of plants from the literature, study sites, and pollen follows the USDA-NRCS Plants Database (2017).

Pollen Extraction

Standard pollen processing methods are described in Faegri et al. (1989) and previous processing methods for pollen derived from insects are in Jones (2012, 2014). In contrast, I extracted pollen from the frass samples using a radically simplified standard palynological process. I added 3.5 ml of 10% KOH (Fisher Scientific, Pittsburgh, PA) to each vial and allowed at least 12 h for the excess organic matter to break down. The sample was spiked with 10 µl of a suspension of polyethylene microspheres (~16 µm diameter, 5.0 × 104 markers/ml ± 8.0% s.d. in 25% KCl; LacCore, Minneapolis, MN). The microspheres served as a standard reference for calculating concentrations. I transferred a 1-ml sample of the KOH-frass extract to a microcentrifuge tube (1.7 ml; C-2170; Denville Scientific, Holliston, MA), vortex-mixed (K-550-G, VMR, Scientific Industries, Inc., Bohemia, NY), then centrifuged at 13,400 rpm for 5 min (Mini-Spin®; Eppendorf, Hamburg, Germany). I decanted the supernatant, added another 1 ml of KOH-frass extract, and repeated the process until the entire sample had been transferred. Each sample was rinsed twice with 1 ml of deionized water, then twice with either 1 ml of *tert*-butanol or isopropanol, in each case agitating the sample, re-centrifuging, and decanting the supernatant. The water removed the remaining KOH and the alcohol dehydrated the sample. The resulting pellet of pollen (plus microspheres) was agitated again, followed by the addition of ~30 µl of silicone oil (200 centipoise mounting medium; Brookfield Engineering Laboratory, Middleboro, MA). Vials were left uncapped overnight to allow any remaining alcohol to

evaporate.

The silicone oil samples were mounted on glass microscope slides with cover slips. The number of pollen grains per sample was estimated by counting the pollen grains and microspheres within three arbitrary passes across the coverslip under a 400× light microscope (E600 brightfield, Nikon Corp., Tokyo, Japan). I photographed the most common pollen grains on a Zeiss Axio Imager.A2 compound microscope with an AxioCam camera (Thornwood, NY) at 400× magnification. I digitally modified the pollen images (using extended focus, increased contrast) (HeliconFocus, Helicon Soft, Ltd., Kharkiv, UKR) for comparison pollen reference material.

I identified pollen grains to genus or species when possible, or grouped them by plant families. Taxonomically unidentified types were defined as morphospecies following characters in Punt et al. (2007). Some pollen types were not found in dichotomous keys of local taxa (Kapp 1969, McAndrews et al. 1973). Some pollen taxa are difficult to differentiate as species due to hybridization, such as species of *Quercus* L. (Fagaceae) (Rushton 1993, Aldrich et al. 2003) and *Crataegus* L. (Rosaceae) (Phipps and Muniyamma 1980, Wrońska-Pilarek et al. 2013). However, pollen grain characters are shared within plant families, allowing types to be grouped as more general classifications (Hebda et al. 1988, Hebda and Chinnappa 1990). For example, *Morus* L. spp. and *Maclura pomifera* (Raf.) C.K. Schneid. were grouped as "Moraceae types". *Betula* L. spp., *Carpinus caroliniana* Walter, and *Ostrya virginiana* (Mill.) K. Koch were denoted as "Betulaceae types". Finally, "Apiaceae types" and "Asteraceae types" contain pollen grains with characters unique to pollen grains in each family (see Kapp 1969). The richness estimates, therefore, likely underrepresent the true plant diversity within frass samples.

Analyses

Estimated pollen grain abundance per sample was calculated by the following equation (from Faegri et al. 1989, Jones 2012, 2014):

$$E = vc \times \left(\frac{p}{m}\right), \text{ where}$$

E = total estimated abundance of pollen grains,

v = volume of markers added (0.01 ml),

c = concentration of markers added (5×10^4 markers/ml),

p = number of observed pollen grains, and

m = number of observed markers.

I calculated averages and standard error (SE) for the abundance and richness of the pollen grains in all beetle frass samples for descriptive purposes. I designated a mean abundance of 1000 pollen grains as an arbitrary threshold to classify species of beetles as pollen-feeding or not. I used fourth-root transformations on abundance data to satisfy assumptions of normality and homogeneous variances (McCune and Grace 2002). For all pollen-feeding species of beetles, I pooled fourth-root transformed abundances into two categories based on collection methods: beetles collected on flowers and beetles collected otherwise (i.e., panel traps, mercury vapor lamps). One-way ANOVA was used to test differences of transformed abundances in both categories. Second, I used a square-root transformation on pollen grains abundances for species of beetles with a sample size of at least 20 individuals. A one-way ANOVA and Student's t-test post hoc analysis were used to test differences among species of palynivorous beetles included in the analysis. All statistical analyses were conducted on JMP statistical software (SAS Institute Inc., Cary, NC).

Next, I calculated the alpha diversity of pollen grains in the frass of beetles collected on flowers. Alpha diversity was calculated using the Shannon-Wiener Index (H) because it captures the relative abundance of species within an assemblage (Shannon 1948). I used the following equation was to calculate the Shannon-Wiener Index:

$$H = \sum \frac{e}{E} \times \ln(\frac{e}{E}) \text{, where}$$

H = index of alpha diversity,

E = total estimated number of pollen grains, and

e = estimated number of pollen grains for a given taxa.

The Shannon-Wiener Index was used for descriptive purposes only.

Fourth, I described the composition of pollen grain taxa by calculating the relative abundances and proportions (mean ± SE) of pollen types for palynivorous beetles collected in traps and at mercury vapor lamps only, and withholding unidentifiable pollen grain types.

To discriminate among the effects of collection date and site on the richness, abundance, and composition of the pollen samples, I analyzed the frass composition of 24 individuals of the most abundant beetle species, *M. caryae*. The individuals equally represented two days and two sites. Beetles originated from the Illinois Forestry Plantation (IFP) and private residence #1 in Urbana (PR1) (see Table 1) on April 17, 2016 and April 25, 2016. IFP and PR1 were classified

as forested and urban habitats, respectively, and located approximately 2.64 km apart. The mean temperature on April 17 and April 25 was 19.4°C and 20°C, respectively. A two-way ANOVA was conducted on the total abundance of pollen grains and richness of pollen grains per day and site with sexes pooled to increase statistical power. Abundance data were fourth-root transformed before analyses to ensure homogeneous variances of residuals and barring unidentifiable pollen grains. Analyses were conducted on JMP statistical software (SAS Institute Inc., Cary, NC).

Next, I conducted permutational MANOVA on the composition or abundances of pollen grain taxa from the fourth-root transformed data for these 24 individuals. S17 Bray-Curtis similarity nonmetric multidimensional scaling was run with 999 permutations of residuals and with the two levels per date and site, removing three beetles with no data. Analyses were conducting using PRIMER 7 and PERMANOVA+ statistical software (PRIMER-E, Quest Research Ltd., Auckland, NZ).

RESULTS

A total of 21 species of cerambycids were collected (18 cerambycines and 3 lepturines). *Megacyllene robiniae* (Forster), *Molorchus bimaculatus bimaculatus* (Say), *Rhopalophora longipes* (Say), *Callimoxys sanguinicollis* (Olivier), *Euderces picipes* (F.), and all lepturines were collected on flowers. All other species were collected using pheromone-baited panel traps, with the exception of six individuals of *Anelaphus pumilus* (Newman), which were collected at a mercury vapor lamp. The samples sizes for each species of beetle and sexes are summarized in Table 2.

Review of Floral Host Records

Thirteen of the 21 study species have been reported previously on flowers (Appendix A). Associated floral hosts total 127 taxa (e.g., genus to subspecies and variety) in 33 plant families across 21 plant orders. Of these floral hosts, 103 were species or varieties with reported growth habits: 50.5% are considered herbaceous or forbs, 13.6% are subshrubs or shrubs, 30.1% are tress/shrubs, 0.02% are trees, and the remaining 4.85% vary in growth habits from herbaceous (or forbs) to vines to shrubs (or subshrubs) (USDA, NRCS 2017). Table 3 details the numbers of floral hosts and proportions of growth habits for floral hosts per species of beetle.

There were 10 cerambycines in the present study that were also reported on flowers in the literature. Seventeen floral taxa (14 species in 10 genera in 6 plant families) have been recorded for *Callimoxys sanguinicollis*. Sixteen floral hosts (14 species in 10 genera in 7 plant families) have been recorded for *Cyrtophorus verrucosus* (Olivier). Thirty-five floral hosts (32 species in 30 genera, in 15 plant families) have been recorded for *Euderces picipes*. Five floral hosts (3 species in 5 genera in 4 plant families) have been recorded for *Euderces pini* (Olivier); however, this species is easily confused with *E. picipes* in coloration (Berlocher et al. 1992, MacRae and Rice 2007). *Hydrangea arborescens* L. (Hydangeaceae) was the only floral host recorded for *Elaphidion mucronatum* (Say) and *Neoclytus mucronatus mucronatus* (F.) (McDowell 2011). Four floral records (4 genera in 2 families) were recorded for *Megacyllene caryae* (Dusham 1921, Gosling 1984, Lingafelter 2007); however, this species of beetle is easily confused with its congener, *Megacyllene robiniae* (Yanega 1996). Five floral hosts (5 species in 2 genera in 1 plant family) have been recorded for *M. robiniae*. Thirty-six floral hosts (30 species in 18 genera

in 8 plant families) have been recorded for *Molorchus b. bimaculatus*. Twenty flora hosts (16 species in 16 genera in 11 plant families) were recorded for *Rhopalophora longipes*.

All three species of lepturines in this study were previously reported on flowers in the literature. Nineteen floral taxa (19 species in 18 genera in 14 plant families) were recorded for *Analeptura lineola* (Say). Eighteen floral taxa (17 species in 16 genera in 11 plant families) were recorded for *Strangalia famelica solitaria* Haldeman. Forty-four floral taxa (42 species in 38 genera in 19 plant families) were recorded for *Typocerus velutinus velutinus* (Olivier).

No floral hosts were reported in the literature for the following long-horned beetles: *Phymatodes amoenus* (Say), *Phymatodes lengi* Joutel, *Phymatodes testaceous* (L.), *Phymatodes varius* (F.), *Neoclytus acuminatus acuminatus* (F.), *Neoclytus caprea* (Say), *Xylotrechus colonus* (F.), and *Anelaphus pumilus*.

Pollen Grain Diversity in Foraging Beetle Frass

I collected five species of cerambycines and three lepturines on the following flowers: *Ageratina altissima* (L.) King & H.E. Robins. (Asteraceae), *Blephilia hirsuta* (Pursh) Benth. (Lamiaceae), *Campanulastrum americanum* (L.) Small (Campanulaceae), *Conium maculatum* L. (Apiaceae), *Cornus drummondii* C.A.Mey. (Cornaceae), *Cornus florida* L. (Cornaceae), *Daucus carota* L. (Apiaceae), *Rosa multiflora* Thunb. (Rosaceae), *Solidago canadensis* L. (Asteraceae), and *Viburnum* L. spp. (Caprifoliaceae). The number of beetles collected on each flower is summarized in Table 4. Beetles were encountered foraging on flowers or *in copula* on flowers. Beetles were primarily collected in the morning and early evening; *Euderces picipes*, *Strangalia f. solitaria*, and *T. v. velutinus* were collected in the early afternoon. *Daucus carota*, *Rosa multiflora*, and *Solidago canadensis* were found in open prairie habitats near forest edges. *Blephilia hirsuta* and *Ageratina altissima* were in the forest interior. All other flower species were located along forest edges.

Relative abundances of pollen grains (untransformed mean) in the frass of foraging beetles exceeded 10,000 for all species. All frass from beetles collected on flowers contained pollen grains. 78%, 86%, and 92% of frass samples from *E. picipes*, *M. b. bimaculatus*, and *T. v. velutinus*, respectively, has an estimated pollen grain abundance that exceeded 1,000. All frass samples of other free-foraging beetles had more than 1,000 estimated pollen grains. The lowest and highest relative abundance of pollen grains (mean ± SE) was observed in *R. longipes* (11,364

± 3,569) and *S. f. solitaria* (89,436 ± 48,393), respectively. Untransformed pollen grain abundances are presented graphically in Fig. 1 and Fig. 2. *C. sanguinicollis* and *M. b. bimaculatus* had three pollen types in their frass, while all the other species had one, on average (Fig. 1).

Micrographs of representative pollen grain taxa are shown in Fig. 3, and taxonomically unidentified morphotypes are shown in Fig. 4. Diversity indices were calculated and presented graphically for pollen grains recovered from the frass of *A. lineola, C. sanguinicollis*, *E. picipes*, and *R. longipes* collected from the flowers of *Cornus drummondii*. I also include the results for *E. picipes* collected on *Conium maculatum* and *Daucus carota*; *M. b. bimaculatus* on *Cornus florida*; *M. robiniae* on *Solidago canadensis*; and *T. v. velutinus* on *Rosa multiflora* (Fig. 5). *C. sanguincollis* appears to show the highest Shannon-Wiener Index (H) compared to the other species of beetles collected on *Cornus drummondii* flowers. Specifically, the Shannon-Wiener Index was >0.8 for *C. sanguinicollis* and <0.25 for the other species on the same plant species. The Shannon-Wiener Index was 0.88 for *M. b. bimaculatus* collected on *Cornus florida* flowers and <0.1 for other species of beetles collected on other flowers.

Many pollen grain taxa were observed in the frass of *C. sanguinicollis* and *M. b. bimaculatus* that were different from the flower where they were collected. For example, morphotype #2 and #7 (Fig. 4) were in the frass of some *C. sanguinicollis* beetles, often in higher proportions than *Cornus drummondii* pollen. Similarly, morphotype #9 was observed in the frass of four *M. b. bimaculatus* beetles. Finally, only one of five *A. lineola* beetle had morphotype #7 pollen in its frass despite being collected on *Cornus drummondii* flowers.

Pollen Grain Diversity in Free-flying Beetle Frass

The abundance and richness of pollen grains are presented graphically for beetles collected in traps and at lights (Fig. 1). These calculations suggest that only four of these species had a mean estimated abundance that exceeded a conservative threshold of 1,000 grains (Fig. 2). I classified *A. pumilus, C. verrucosus*, *E. pini*, and *M. caryae* as palynivorous. Moreover, 41%, 59%, 67%, and 55% of frass samples from *A. pumilus*, *C. verrucosus*, *E. pini*, and *M. caryae*, respectively, contained more than 1,000 estimated pollen grains. I did not consider the other species of beetles collected as palynivorous, which includes all *Neoclytus* spp., all *Phymatodes* spp., *Elaphidion mucronatum*, and *Xylotrechus colonus*. The mean richness of pollen grains in

the frass of palynivorous beetles was 2 (i.e., *A. pumilus*) and 3.5 (i.e., *M. caryae*), and less than 1 for all non-pollen-feeding species. The assumption of homogeneous variances was met for fourth-root transformed abundance (Brown-Forsythe; F = 1.82, $P = 0.1787$). I found that the pollen grain abundance (untransformed) in the frass of palynivorous beetles on flowers was four-fold higher than palynivorous beetles collected otherwise (Fig. 2A; one-way ANOVA, fourth-root transformed abundance; df = 1, F = 88.88, $P < 0.001$).

I tested differences in pollen grain abundance in the frass of 6 palynivorous beetles with adequate sample sizes (i.e., $n \geq 20$) regardless of trapping method. I conducted on one-way ANOVA on *M. robiniae*, *E. picipes*, *E. pini*, *M. caryae*, *C. verrucosus*, and *A. pumilus*. Assumption of homogeneous variances were met for square-root transformed abundances prior to the analysis (Brown-Forsythe; F = 1.48, $P = 0.1966$). These results indicated a significant difference among six species (Fig. 2A; one-way ANOVA, square-root transformed; df = 5, F = 19.23, $P < 0.0001$). Student's *t*-test post hoc analysis indicated that *A. pumilus*, *C. verrucosus*, *E. pini*, and *M. caryae* were similarly low in pollen grain in square-root transformed abundances (untransformed mean abundance was between 9,000 and 16,000 pollen grains). *E. picipes* and *M. robiniae* were each significantly different and had an untransformed mean of 34,000 and 78,000 pollen grains, respectively. The graphical representation of untransformed mean abundance per species of beetle and post hoc analysis on square-root transformed abundances is in Fig. 2B.

The relative mean abundances and mean proportions were calculated for pollen grain taxa in the frass of *A. pumilus*, *C. verrucosus*, *E. pini*, and *M. caryae*, which serve as descriptors in the absence of statistical analyses. *Vitis* L. (Vitaceae), *Quercus* L. (Fagaceae), and *Juglans nigra* L. (Juglandaceae) appear to have a high relative abundances and proportions from the frass of *A. pumilus*; however, 9 other pollen types were also observed. *C. verrucosus* frass had a pollen richness of 20, including pollen from *Viburnum* L. (Caprifoliaceae), *Acer* L. (Sapindaceae), and *Quercus* as the most abundant pollen taxa. *Quercus*, *Viburnum*, and Moraceae-type pollens (i.e., *Morus* spp., *Maclura pomifera*) occurred in the highest mean proportion across frass samples from *C. verrucosus*. *E. pini* frass had a pollen richness of 19, including pollen from *Cercis canadensis* L. (Fabaceae), *Quercus*, and *Fraxinus* L. (Oleaceae) appearing to have the highest relative abundances and *Quercus*, *Acer*, and *Crataegus* L. (Rosaceae) appearing to have the highest relative proportions. *M. caryae* frass had a pollen richness of 26, including pollen from *Crataegus*, *Platanus occidentalis* L. (Platanaceae), and *Acer* with the highest relative abundances

and *Crataegus*, *Quercus*, and *Fraxinus* with highest relative proportions. These data are summarized in Table 5 and associated pollen grain images are show in Fig. 3 and Fig. 4.

Pollen Grain Diversity in *Megacyllene caryae*

Overall, the two-way ANOVA indicated a significant effect by date and site on the abundance (fourth-root transformed) of pollen grains from *M. caryae* frass (df = 3, F = 10.91, *P* = 0.0002). There was a higher abundance of pollen grains from frass samples from April 25, 2016 compared to April 17, 2016 (df = 1, F = 24.46, *P* < 0.0001). Abundance was higher in the urban site (i.e., Private residence #1 in Urbana, IL) than in the forest site (i.e., Illinois Forestry Plantation; df = 1, F = 7.86, *P* = 0.011). Overall, the two-way ANOVA showed a significant effect of date and location on the richness of pollen types (df = 3, F = 5.58, *P* = 0.006). There was a higher richness of pollen types in the frass of *M. caryae* collected on the later date than the earlier date (df = 1, F = 14.29, *P* = 0.0012), but no significant difference of pollen richness in the frass of beetles collected at either study site (df = 1, F = 2.35, *P* = 0.1411). There was no significant interaction between collection date and study site pollen grain abundance (df = 1, F = 0.40, *P* = 0.5367) and richness (df = 1, F = 0.09, *P* = 0.7624). Table 6 summarizes the ANOVA reports and relative abundances and richness pollen grains in the frass of *M. caryae* for both sites and dates.

Statistical analyses via PERMANOVA indicated a significant effect of date (df = 1, F = 4.67, *P* = 0.002) and site (df = 1, F = 2.45, *P* = 0.006) on the composition of pollen grains from *M. caryae* (barring 3 samples). No significant interaction between date and site was observed (df = 1, F = 1.83, P = 0.084). Noteworthy pollen types include *Quercus*, *Liquidambar styraciflua* L. (Altingiaceae), morphotype #4, and morphotype #10 because they were observed in frass samples from April 25, 2016 at both sites. Additionally, *Crataegus*, *Quercus*, *Acer*, and *Celtis occidentalis* L. (Cannabaceae) were observed in both sites on April 17. *Quercus* was higher in frass samples on the later date than the earlier date, whereas *Acer* was higher in the earlier date than the later date. *Lonicera* L. (Caprifoliaceae) and *Salix* L. (Salicaceae) were observed in samples from IFP on April 25, 2016 only. *Fraxinus* pollen was found in all samples except for those at IFP on April 17, 2016. *Platanus occidentalis* pollen was found in all sample except for PR1 on April 17, 2016. *Pinus* L. (Pinaceae) and Betulaceae-type pollens, although in low abundances, were in samples on April 25, 2016 at both sites. No pollen grains were recovered

from the frass of 2 beetles on April 17, 2016 at IFP and 1 beetle from PR1 on April 17, 2016. Nonmetric multidimensional scaling (NMDS) (2D stress: 0.09) show how the composition of pollen grains recovered from the frass of the 21 samples differentiate and cluster per sampling date and study site (Fig. 6). Sex was not analyzed due to unequal replication, but it was included in the NMDS plots for descriptive purposes.

DISCUSSION

Overall, these results provide evidence of palynivory in 12 of 21 of the study species. Thirteen of the 21 species were previously reported on feeding on flowers in the literature; however, 2 of these species, *Elaphidion mucronatum* (n = 32) and *Neoclytus m. mucronatus* (n = 21), showed no evidence of palynivory in the present study. However, new floral host associations were described for several known palynivorous beetles, such as the lepturines, *Cyrtophorus verrucosus*, *Euderces* spp., and *Megacyllene caryae*. Multiple plant species are represented in the frass of many palynivores, suggesting that these beetles forage on more than one floral host during their lifetime. Finally, I provide evidence of palynivory in *Anelaphus pumilus*, which has no floral host records in the literature to my knowledge. Given the limits of my sampling, it is difficult to claim floral host associations of beetles with certainty; however, in some cases, pollen grains in the frass of beetles corroborate floral hosts described in the literature.

These results suggest a bias in floral records toward flowering plants that are accessible to researchers (i.e., herbaceous plants, shrubs, and small trees; Table 3). In contrast, pollen grains extracted from the frass of beetles collected in traps, was often that of large trees. For example, pollen grains from species of *Quercus*, *Acer*, and *Fraxinus*, as well as *Platanus occidentalis* and *Juglans nigra*, were recovered from the frass of the four palynivorous beetles collected in traps. Several species of cerambycids can be preferentially collected in the forest canopy using semiochemicals (Graham et al. 2012b, Schmeelk et al. 2016, Wong and Hanks 2016), flight-intercept traps (Ulyshen and Hanula 2007), and fumigation (Krinsky and Godwin 1996). Many beetles are known to oviposit on tree branches presumably in the canopy (Yanega 1996), my results show that they also forage on pollen in the canopy. The sampling bias inherent to floral host records would also explain why *M. caryae* has yet to be observed feeding on *Crataegus* in nature, as well as the absence of floral hosts associated with *A. pumilus*. Beetles collected by hand were also found foraging on floral hosts that differed from records in the literature. For example, I collected a single *E. picipes* on *Campanulastrum americanum*; *S. f. solitaria* and *T. v. velutinus* on *Blephilia hirsuta*; and *T. v. velutinus* on *Ageratina altissima*, among others.

The high relative diversity of pollen grains from the frass of some cerambycids suggests that these beetles visit numerous flower species in their lifetime. This was evidenced by the qualitatively high evenness of pollen grains in the frass of *Callimoxys sanguinicollis* and

Molorchus b. bimaculatus compared to other beetles collected on flowers. Generalist palynivory has been described by McDowell (2011) who noticed that the same species of cerambycids were found on *Daucus carota* and *Hydrangea arborescens*, which were in bloom at the same time. Moreover, the review of floral host records provides evidences of several species that overlap in their blooming phenology, for example, *Crataegus* spp. (Phipps and Muniyamma 1980) and *Cornus florida* (Reader 1975). The timing and duration of anthesis overlap for several trees in Illinois, such as *Acer saccharum*, *Quercus*, and *Juglans nigra* (C. Augspurger pers. com.); however, the timing and duration vary annually and between plant species, as described in other temperate regions (Jack 1931, Menzel et al. 2006, Ziello et al. 2012). My results suggest that individual beetles may consume pollen from numerous flower species during their adult stage and, as a population, appear to exhibit generalist feeding strategies during their seasonal activity period.

The amount and types of pollen consumed by *M. caryae* were affected by the season and habitat. The number of pollen grains in the frass of *M. caryae* beetles was higher at the urban site and on the later date, and a higher richness of pollen grains was observed in the frass of beetles collected on the later date. The seasonal activity period of *M. caryae* extends from April to early May in east central Illinois (Hanks et al. 2014) during which time several flowering plants are sexually mature, such as *Crataegus* (Phipps and Muniyamma 1980) and *Quercus* (C. Augspurger, pers. com.). Metropolitan areas exhibit a phenomenon known as "urban heat islands," which causes an earlier anthesis of flowering plants in more urbanized areas than in rural or less urban environments (Chuine et al. 1999, Ziello et al. 2012, Ríos et al. 2016). Moreover, the richness and diversity of flowering plants in urban areas are lower than in the countryside (Vakhlamova et al. 2014, Swan et al. 2017). It is unclear if this pattern of plant diversity is consistent for trees and shrubs alone. Habitats cannot be considered isolated because the use of long-range sex-aggregation pheromones may attract beetles outside of the study site. For example, downwind of the IFP site is a recreational park with numerous spring-blooming trees and shrubs not found in the site itself.

Conspicuous coloration, diel phenology, and seasonal phenology could be good indicators of palynivory in cerambycid beetles. Most of the palynivorous cerambycids in the present paper are among the first to emerge in the spring (Mitchell et al. 2015). In the spring, the return of migratory, insectivorous birds, such as warblers and vireos, could be a strong selective

pressure on adult beetles in the spring (Strode 2015). Yanega (1996) posits that crypsis and mimicry likely evolved in response to predation. As a result of predation, many palynivorous lepturines and cerambycines are conspicuously colored and diurnal (Linsley 1959). For example, *Megacyllene caryae* and *M. robiniae* resemble stinging wasps (Hymenoptera) and produce alarm pheromones of stinging wasps (Mitchell et al. 2017). Moreover, palynivorous *Euderces picipes* and *E. pini* are mimics of ants (Hymenoptera: Formicidae; Berlocher et al. 1992) and diurnal (pers. obs., Mitchell et al. 2015). Noteworthy exceptions are two other spring-emerging species, *Anelaphus pumilus* and *Neoclytus caprea*; the former is nocturnal and palynivorous, whereas the latter is diurnal (Mitchell et al. 2015), seemingly aposematic (e.g., black and yellow coloration), and does not feed on pollen.

I reaffirm the position held by Yanega (1996) who argued that cerambycids are ideal for biomonitoring. The larval hosts of cerambycid beetles vary taxonomically, structurally (e.g., branches), and nutritonally (e.g., living, decomposed). Attention is often given to cerambycid checklists to understand local or regional beetle community assemblages (McCorquodale and Bondrup-Nielsen 2004). This, in combination with information on larval hosts for beetle species, could indicate the quality of forest ecosystems. Many factors affect cerambycid assemblages in forest ecosystems, such as tree-fall gaps (Bouget 2005), vegetative community structure (Fayt et al. 2006, Meng et al. 2013), forest edge structure (Wermelinger et al. 2007), and habitat continuity (Brin et al. 2016). Floral host records add to our understanding of the natural history and feeding behaviors of cerambycid beetles, which may inform conservation strategies.

Several species of long-horned beetles are serious economic pests (Solomon 1995). Long-horned beetles possess traits that may influence their ability to colonize areas inside and outside of their native range (Crawley 1986, Lawton and Brown 1986). Dietary requirements and polyphagy may contribute to their success as invaders (Raje et al. 2016). A dependence on pollen-feeding as adults may influence the ability of a species to invade new areas. The positive fitness effects observed in *Phoracantha* spp. (Millar et al. 2003), for example, emphasizes how feeding on suitable pollen may enhance the ability of a species to establish and invade. Furthermore, anthophily seems to facilitate mate-location in some beetles (Michelsen 1963). Additional investigations are needed to describe the physiological effects of pollen-feeding, such as reproductive maturation, on potentially invasive cerambycid beetles.

In conclusion, I applied interdisciplinary methods in palynology and forest pest management to characterize the diet of adult long-horned beetles. To accomplish this, I developed a method to extract pollen from insect frass, which is substantially simpler, and safer, than traditional palynological methods used in entomology (Jones 2012, 2014). These results indicate that some cerambycids do feed on pollen as adults. To the list of palynivorous cerambycids, this study adds two species that had not previously been described as feeding on pollen in nature. I also recovered a variety of pollen grains from hardwood trees in the frass of palynivorous cerambycids, which substantially expands the floral hosts associated with several species of long-horned beetles. Finally, the results of this study inform the basic biology and behavior of long-horned beetles, which enhances understanding of palynivory in beetles and forest pest management and at the same time builds on the body of knowledge about the natural history of these understudied beetles.

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TABLES AND FIGURES

Table 1. Summary of the study sites. The number of individual beetles collected at each site is listed under column titled "n". No site location was recorded for 8 specimens.

State/County	Site	Latitude, longitude	n	Area (ha)
IL/Champaign	Brownfield Woods[a]	40.1452°, -88.1657°	16	26
	Busey Woods[b]	40.1271°, -88.2134°	5	24
	South Arboretum Woods[a]	40.0852°, -88.2167°	51	9
	Illinois Forestry Plantation[a]	40.0780°, -88.2111°	96	16
	Nettie Hart Memorial Woods[a]	40.2297°, -88.3579°	30	16
	Private residence #1 in Urbana	40.0996°, -88.2169°	95	<0.1
	Private residence #2 in Urbana	40.0971°, -88.2033°	87	<0.1
	Private residence #3 in Urbana	40.1349°, -88.1757°	52	<0.1
	Private residence #4 in Urbana	40.1073°, -88.2052°	39	<0.1
	Private residence #5 in Urbana	40.1147°, -88.2146°	23	<0.1
	Private residence in Champaign	40.1017°, -88.2862°	19	<0.1
	Trelease Woods[a]	40.1349°, -88.1428°	7	25
IL/Grundy	Mazonia-Braidwood State Fish and Wildlife Area[c]	41.2154°, -88.2729°	12	412
IL/Piatt	Robert Allerton Park and Retreat Center[a]	39.9853°, -88.6501°	78	600
IL/Vermillion	Forest Glen Preserve[d]	40.0151°, -87.5677°	13	728
	Muncie	40.1149°, -87.8389°	1	n/a
	Vermillion River Observatory[a]	40.0656°, -87.5613°	10	193
IN/Putnam	Private residence in Reelsville	39.5726°, -86.9610°	8	15

[a] University of Illinois (http://research.illinois.edu/cna/)

[b] Urbana Park District (http://www.urbanaparks.org/)

[c] Illinois Department of Natural Resources (http://www.dnr.illinois.gov/)

[d] Vermilion County Conservation District (http://www.vccd.org/)

Table 2. Numbers of cerambycid beetles and collection method. Collection methods are manually collected from flowers (hc), pheromone-baited traps (pt), and mercury vapor lamp (mv).

Taxonomy	Method	Male	Female	Unknown	Total
Cerambycinae					
Anaglyptini					
Cyrtophorus verrucosus (Olivier)	pt	16	16		**32**
Callidiini					
Phymatodes amoenus (Say)	pt	9	8	1	**18**
Phymatodes lengi Joutel	pt	14	26	9	**49**
Phymatodes testaceus (L.)	pt	10	12	5	**27**
Phymatodes varius (F.)	pt	15	13	4	**32**
Clytini					
Megacyllene caryae (Gahan)	pt	93	79	2	**174**
Megacyllene robiniae (Forster)	hc	9	11		**20**
Neoclytus acuminatus acuminatus (F.)	pt	7	16	1	**24**
Neoclytus caprea (Say)	pt	8	18	5	**31**
Neoclytus mucronatus mucronatus (F.)	pt	8	11	2	**21**
Xylotrechus colonus (F.)	pt	13	17	1	**31**
Elaphidiini					
Anelaphus pumilus (Newman)	pt, mv	11	2	9	**22**
Elaphidion mucronatum (Say)	pt	19	9	4	**32**
Molorchini					
Molorchus bimaculatus bimaculatus Say	hc		7		**7**
Rhopalophorini					
Rhopalophora longipes (Say)	hc	5	9		**14**
Stenopterini					
Callimoxys sanguinicollis (Olivier)	hc	3	2		**5**
Tillomorphini					
Euderces picipes (F.)	hc	15	10	2	**27**
Euderces pini (Olivier)	pt	19	30	9	**58**
Lepturinae					
Lepturini					
Analeptura lineola (Say)	hc	2	3		**5**
Strangalia famelica solitaria Haldeman	hc	6	2	1	**9**

Table 2 (continued)

Taxonomy	Method	Male	Female	Unknown	Total
Typocerus velutinus velutinus (Olivier)	hc	4	7	1	**12**
TOTAL					**650**

Table 3. Summary of floral hosts associated with the study species in the literature (from Appendix A). Growth habit is characterized as herbaceous or forbs (H), vine (V) shrub or subshrub (S), tree (T), or a combination of growth habits. The proportion of growth habits was calculated from the total records per study species (in parentheses).

Study Species	Number of Floral Hosts								
	Total	Taxonomy			Growth Habit				
		Families	Genera	Spp.	H	H/S/V	S	T/S	T
Cerambycinae									
Callimoxys sanguinicollis	**17**	6	10	14	4 (0.23)	1 (0.06)	2 (0.12)	7 (0.41)	0 (0)
Cyrtophorus verrucosus	**16**	7	10	14	3 (0.19)	0 (0)	3 (0.19)	8 (0.5)	0 (0)
Elaphidion mucronatum	**1**	1	1	1	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)
Euderces picipes	**35**	15	30	32	16 (0.46)	2 (0.06)	7 (0.2)	7 (0.2)	0 (0)
Euderces pini	**5**	4	5	3	1 (0.2)	0 (0)	1 (0.2)	1 (0.2)	0 (0)
Megacyllene caryae	**4**	3	4	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Megacyllene robiniae	**5**	1	2	5	5 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Molorchus b. bimaculatus	**36**	8	18	30	5 (0.14)	0 (0)	5 (0.14)	20 (0.56)	1 (0.03)
Neoclytus m. mucronatus	**1**	1	1	1	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)
Rhopalophora longipes	**20**	11	16	16	6 (0.3)	1 (0.05)	3 (0.15)	3 (0.15)	1 (0.05)
Lepturinae									
Analeptura lineola	**19**	14	18	19	11 (0.58)	0 (0)	5 (0.26)	3 (0.16)	0 (0)
Strangalia f. solitaria	**18**	11	16	17	6 (0.33)	1 (0.06)	4 (0.22)	4 (0.22)	0 (0)

Table 3 (continued)

Study Species	Number of Floral Hosts								
	Total	Taxonomy			Growth Habit				
		Families	Genera	Spp.	H	H/S/V	S	T/S	T
Typocerus v. velutinus	**44**	19	38	42	27 (0.61)	3 (0.07)	7 (0.16)	4 (0.11)	0 (0)

Table 4. Numbers of long-horned beetles collected on flowers.

Floral Host Taxonomy	Cerambycinae					Lepturinae		
	Callimoxys sanguinicollis	*Euderces picipes*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Rhopalophora longipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Apiales: Apiaceae								
Conium maximum L.		6						
Daucus carota L.		7					4	2
Asterales: Asteraceae								
Ageratina altissima King & H.E. Robins								1
Solidago canadensis L.			20					
Campanulales: Campanulaceae								
Campanulastrum americanum (L.) Small		1						
Cornales: Cornaceae								
Cornus drummondii C.A.Mey.	5	11			14	5	1	
Cornus florida L.				7				
Dipsacales: Caprifoliaceae								
Viburnum L. sp.		2						
Lamiales: Lamiaceae								
Blephilia hirsuta (Pursh) Benth.							3	2
Rosales: Rosaceae								
Rosa multiflora Thunb.							1	7
Total	**5**	**28**	**20**	**7**	**14**	**5**	**9**	**12**

Table 5. Mean (± SE) abundance and proportion of pollen grains that were in the frass of free-flying cerambycids. Pollen grains are from 28 plant taxa in total, which includes 6 morphotypes and 22 genera across 23 families and 16 orders. Abundance values are listed above the proportions (in parentheses). Cell values are bolded for mean abundances exceeding 100, for reference.

Floral Host Taxonomy	Beetle Species			
	Anelaphus pumilus	*Cyrtophorus verrucosus*	*Euderces pini*	*Megacyllene caryae*
Morphotypes				
Type 1		**259 ± 224**		90 ± 90
		(0.04 ± 0.03)		(0.01 ± 0.01)
Type 2			**332 ± 272**	
			(0.03 ± 0.02)	
Type 4				**497 ± 337**
				(0.02 ± 0.01)
Type 5				**193 ± 193**
				(0.01 ± 0.01)
Type 8		**679 ± 428**		
		(0.07 ± 0.04)		
Type 10				**560 ± 334**
				(0.02 ± 0.01)
Apiales				
Apiaceae				
(Type)		3.91 ± 3.84		0.29 ± 0.29
		(0.02 ± 0.02)		(0.00 ± 0.00)
Asterales				
Asteraceae				
(Type 1)			17 ± 17	
			(0.01 ± 0.01)	
(Type 2)			4.72 ± 3.13	5.27 ± 1.89
			(0.00 ± 0.00)	(0.00 ± 0.00)
Cornales				
Cornaceae				
Cornus L.		70 ± 51	44 ± 44	
		(0.03 ± 0.02)	(0.01 ± 0.01)	

Table 5 (continued)

Floral Host Taxonomy	Beetle Species			
	Anelaphus pumilus	*Cyrtophorus verrucosus*	*Euderces pini*	*Megacyllene caryae*
Dipsacales				
Caprifoliaceae				
Lonicera L.		**792 ± 779**		94 ± 68
		(0.03 ± 0.03)		(0.01 ± 0.01)
Viburnum L.	15.15 ± 10.22	**3,811 ± 2,039**		38 ± 17
	(0.00 ± 0.00)	**(0.12 ± 0.05)**		(0.02 ± 0.01)
Fabales				
Fabaceae				
Cercis canadensis L.			**3,565 ± 3,290**	
			(0.03 ± 0.02)	
Fagales				
Betulaceae				
(Type)		29 ± 17	**477 ± 237**	**102 ± 23**
		(0.01 ± 0.01)	**(0.06 ± 0.03)**	**(0.04 ± 0.01)**
Alnus Mill.				0.65 ± 0.46
				(0.00 ± 0.00)
Fagaceae				
Carya Nutt.	20 ± 12	24 ± 13	2.46 ± 2.44	6.68 ± 5.75
	(0.01 ± 0.0)	(0.02 ± 0.02)	(0.00 ± 0.00)	(0.00 ± 0.00)
Quercus L.	**2,236 ± 1,448**	**894 ± 477**	**3,226 ± 1,344**	**638 ± 151**
	(0.22 ± 0.08)	**(0.16 ± 0.05)**	**(0.23 ± 0.05)**	**(0.21 ± 0.02)**
Juglandaceae				
Juglans nigra L.	**1,220 ± 876**	**190 ± 99**	6.35 ± 3.62	65 ± 55
	(0.21 ± 0.07)	**(0.06 ± 0.02)**	(0.01 ± 0.01)	(0.01 ± 0.01)
Lamiales				
Oleaceae				
Fraxinus L.	2.53 ± 2.47	87 ± 41	**2,668 ± 2,270**	**932 ± 463**
	(0.05 ± 0.04)	(0.04 ± 0.02)	**(0.07 ± 0.03)**	**(0.09 ± 0.02)**

Table 5 (continued)

Floral Host Taxonomy	Beetle Species			
	Anelaphus pumilus	*Cyrtophorus verrucosus*	*Euderces pini*	*Megacyllene caryae*
Magnoliales				
Annonaceae				
Asimina triloba (L.) Dunal		46 ± 43 (0.02 ± 0.01)		
Magnoliaceae				
Liriodendron tulipifera L.	7.58 ± 7.40 (0.00 ± 0.00)			
Magnolia L.				52 ± 52 (0.00 ± 0.00)
Malpighiales				
Salicaceae				
Salix L.	16.67 ± 10.29 (0.01 ± 0.00)	2.60 ± 2.56 (0.00 ± 0.00)	3.88 ± 2.71 (0.00 ± 0.00)	52 ± 18 (0.02 ± 0.01)
Malvales				
Tiliaceae				
Tilia americana L.				0.36 ± 0.36 (0.00 ± 0.00)
Pinales				
Cupressaceae				
(Type)				1.01 ± 0.77 (0.00 ± 0.00)
Pinaceae				
Pinus L.	32 ± 16 (0.05 ± 0.03)	36 ± 19 (0.01 ± 0.01)	16 ± 5.95 (0.00 ± 0.00)	28 ± 6.44 (0.02 ± 0.01)
Proteales				
Platanaceae				
Platanus occidentalis L.		8.93 ± 7.73 (0.00 ± 0.00)	**112 ± 72** **(0.03 ± 0.01)**	**1,908 ± 1,773** **(0.06 ± 0.01)**
Rosales				

Table 5 (continued)

Floral Host Taxonomy	Beetle Species			
	Anelaphus pumilus	*Cyrtophorus verrucosus*	*Euderces pini*	*Megacyllene caryae*
Cannabaceae				
Celtis occidentalis L.			**1,012 ± 820**	**701 ± 628**
			(0.05 ± 0.02)	**(0.03 ± 0.01)**
Moraceae				
(Type)	67 ± 33	**640 ± 490**	35 ± 19	33 ± 8.34
	(0.05 ± 0.03)	**(0.08 ± 0.04)**	(0.00 ± 0.00)	(0.02 ± 0.01)
Rosaceae				
Crataegus L.		18 ± 18	**736 ± 468**	**3,441 ± 1,131**
		(0.00 ± 0.00)	**(0.10 ± 0.03)**	**(0.23 ± 0.03)**
Ulmaceae				
Ulmus L.	1.89 ± 1.85	7.81 ± 7.69	**612 ± 423**	51 ± 22
	(0.00 ± 0.00)	(0.00 ± 0.00)	**(0.03 ± 0.02)**	(0.02 ± 0.01)
Sapindales				
Sapindaceae				
Acer L.		**3,220 ± 2,711**	**2,333 ± 889**	**1,091 ± 840**
		(0.07 ± 0.04)	**(0.16 ± 0.04)**	**(0.05 ± 0.01)**
Saxifragales				
Altingiaceae				
Liquidambar styraciflua L.		3.13 ± 3.08	**321 ± 183**	55 ± 22
		(0.00 ± 0.00)	**(0.07 ± 0.03)**	(0.01 ± 0.00)
Vitales				
Vitaceae				
Vitis L.	**5,994 ± 3,901**			
	(0.23 ± 0.09)			

Table 6. Summary of two-way ANOVA on the date and site on the relative abundance (fourth-root transformed) and richness of pollen grains from the frass of *Megacyllene caryae*. Untransformed abundance means and SE data are provided and fourth-root transformed abundance means and SE are in parentheses. Statistical analyses were conducted on fourth-root transformed abundance data. *P*-values are simplified as follows: ≥ 0.05 ("ns"), ≤ 0.05 ("*"), ≤ 0.01 ("**"), ≤ 0.001 ("***"), and ≤ 0.0001 ("****"). Private residence #1 in Urbana, IL and Illinois Forestry Plantation are abbreviated as "PR1" and "IFP," respectively. The two-way output for date and site interaction is denoted as "Date*Site."

	Abundance					**Richness**				
	Mean	SE	df	F	*P*	Mean	SE	df	F	*P*
Model			**3**	**10.91**	***			**3**	**5.58**	**
Date										
April 17, 2016	1,329	549	**1**	**24.46**	****	1.58	0.58	**1**	**14.29**	**
	(4.25)	(0.89)								
April 25, 2016	20,291	5032				4.67	0.58			
	(10.49)	(0.89)								
Site										
PRI (urban)	15,348	4,617	**1**	**7.86**	*	3.75	0.72	**1**	**2.35**	ns
	(9.14)	(0.89)								
IFP (forest)	6,272	3,982				2.5	0.72			
	(5.60)	(0.89)								
Date*Site			**1**	**0.40**	ns			**1**	**0.09**	ns

Figure 1. Relative abundances and richness of pollen grains from the frass of long-horned beetles. Dark and light shading denotes cerambycines and lepturines, respectively. Hatched and solid fill denotes beetles collected on flowers and other methods (i.e., panel traps, mercury vapor lamp), respectively. **A)** Untransformed abundance of pollen grains (mean ± SE) per species of beetle. **B)** Richness of pollen grains (mean ± SE) per species of beetle. Filled (•) and unfilled (◦) circles denote the maximum and minimum observed richness, respectively.

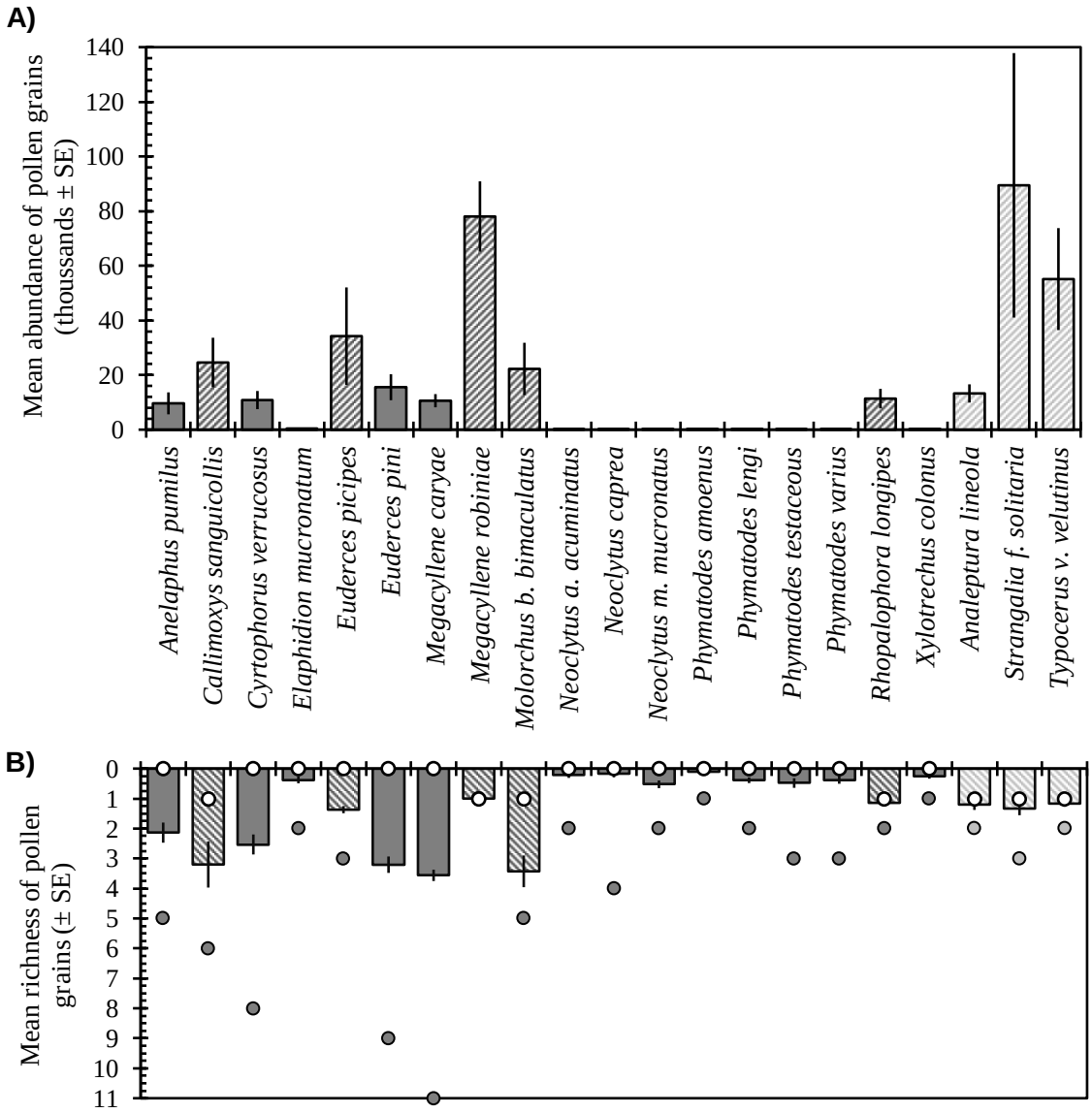


Figure 2. Untransformed abundances of pollen grains (mean ± SE) from the frass of long-horned beetles. Hatched and solid fill bars denote beetles collected on flowers and other methods (i.e., panel traps, mercury vapor lamp), respectively. **A)** Abundance of pollen grains was significantly different (fourth-root transformed; df = 1, F = 88.88, $P < 0.001$) between palynivorous beetles collected on flowers and from other methods. **B)** Beetle species with letters in the heading were included in analyses. Species with different letters are significantly different (square-root transformed; df = 5, F = 19.2303, $P < 0.0001$; Student's *t*-test, $\alpha = 0.05$). Dark and light shading denotes cerambycines and lepturines, respectively. Solid and hatched fill same as described earlier. **C)** Relative richness of pollen grains in the frass of palynivorous beetles.

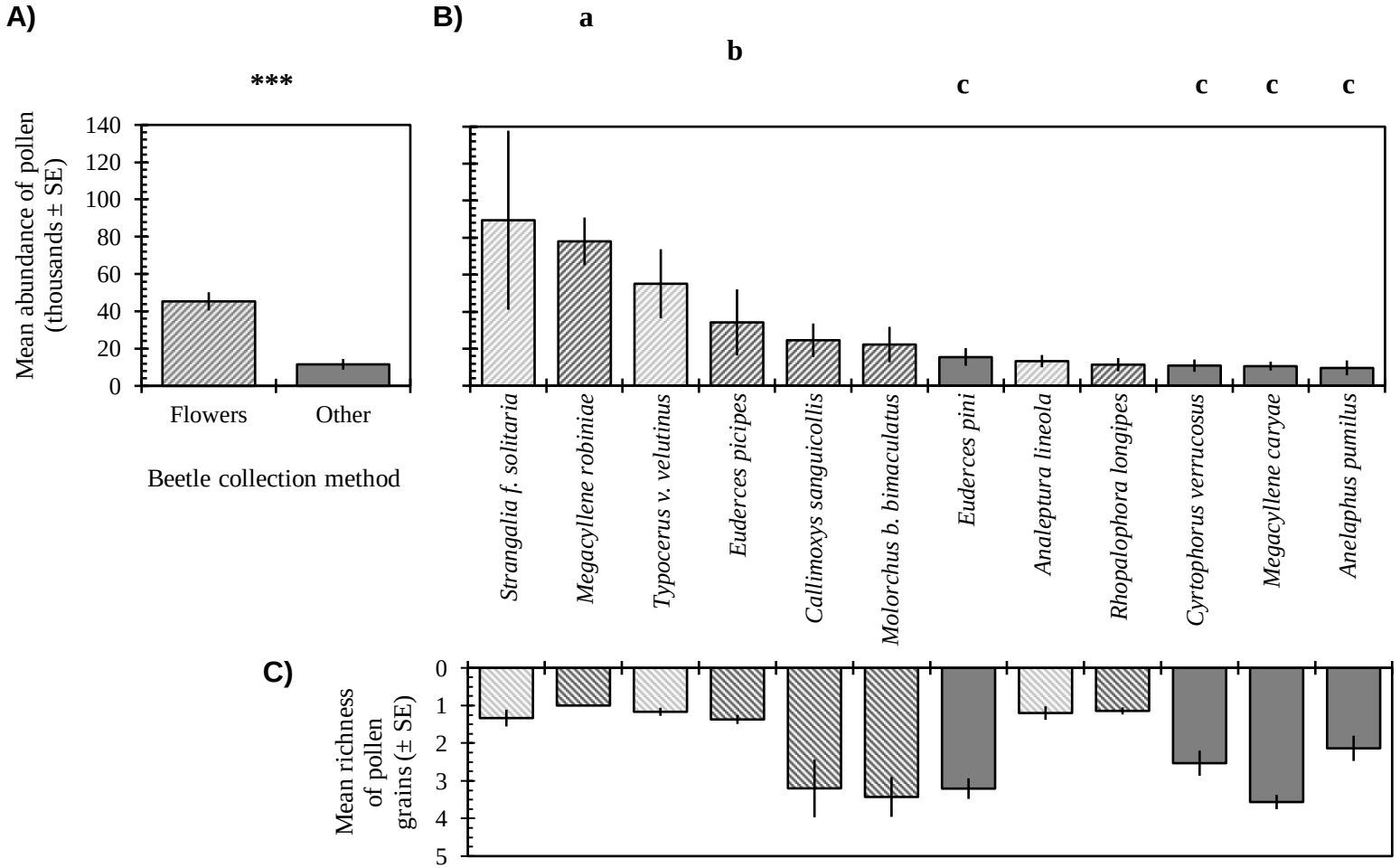


Figure 3. Representative micrographs of dominant pollen grains recovered from the frass of cerambycid beetles. Micrographs acquired under LED lighting at 400 magnification, modified. Arranged taxonomically (order in bold). Orientation abbreviated: **pv** = polar view, **ev** = equatorial view, and **ov** = oblique view, when applicable. Asterisks (*) signify pollen grains from beetles collected on flowers. Swords (†) signify pollen grains fed to *Cyrtophorus verrucosus* in a laboratory setting (unpublished data). Scale bar = 20 µm. **Apiales**. Apiaceae: *Conium maculatum** (L.) ev (A); *Daucus carota** L. ev (B). **Asterales**. Asteraceae: *Ageratina altissima** (L.) King & H.E.Robins. pv (C), ev (D); Asteraceae type 1 pv (E), ev (F); *Solidago canadensis** L. ov (G), ev (H); Campanulaceae: *Campanulastrum americanUM** L. pv (I). **Cornales**. Cornaceae: *Cornus drummondii** C.A.Mey. pv (J), ev (K); *C. florida** L. pv (L), ov (M). **Dipsacales**. Caprifoliaceae: *Lonicera* L. pv (N), ev (O); *Viburnum** L. pv (P), ev (Q). **Fabales**. Fabaceae: *Cercis canadensis* L. pv (R), ev (S). **Fagales.** Betulaceae: Betulaceae-types pv (T); Fagaceae: *Quercus* L. pv (U), ev (V); *Q. macrocarpa*† Michx. ov (W), ev (X); Juglandaceae: *Juglans nigra* L. pv (Y), ev (Z). **Lamiales.** Lamiaceae: *Blephilia hirsuta** (Pursh) Benth. pv (a), ev (b); Oleaceae: *Fraxinus* L. pv (c), ev (d). **Magnoliales.** Annonaceae: *Asimina triloba* (L.) Dunal. pv (e); Magnoliaceae: *Magnolia* L. ev (f). **Malpighiales.** Salicaceae: *Salix* L. ev (g). **Malvales.** Tiliaceae: *Tilia americana* L. pv (h). **Proteales.** Platanaceae: *Platanus occidentalis* L. pv (i), ev (j). **Rosales.** Cannabaceae: *Celtis occidentalis* L. pv (k), ov (l); Moraceae: Moraceae-types ov (m); Rosaceae: *Crataegus* Tourn. pv (n), ev (o); *Rosa multiflora** L. pv (p), ev (q); Ulmaceae: *Ulmus* L. pv (r), ev (s). **Sapindales.** Sapindaceae: *Acer* L. ov (t), ev (u). **Saxifragales.** Altingiaceae: *Liquidambar styraciflua* L. ev (v). **Vitales.** Vitaceae: *Vitis* L. pv (x), ev (y).

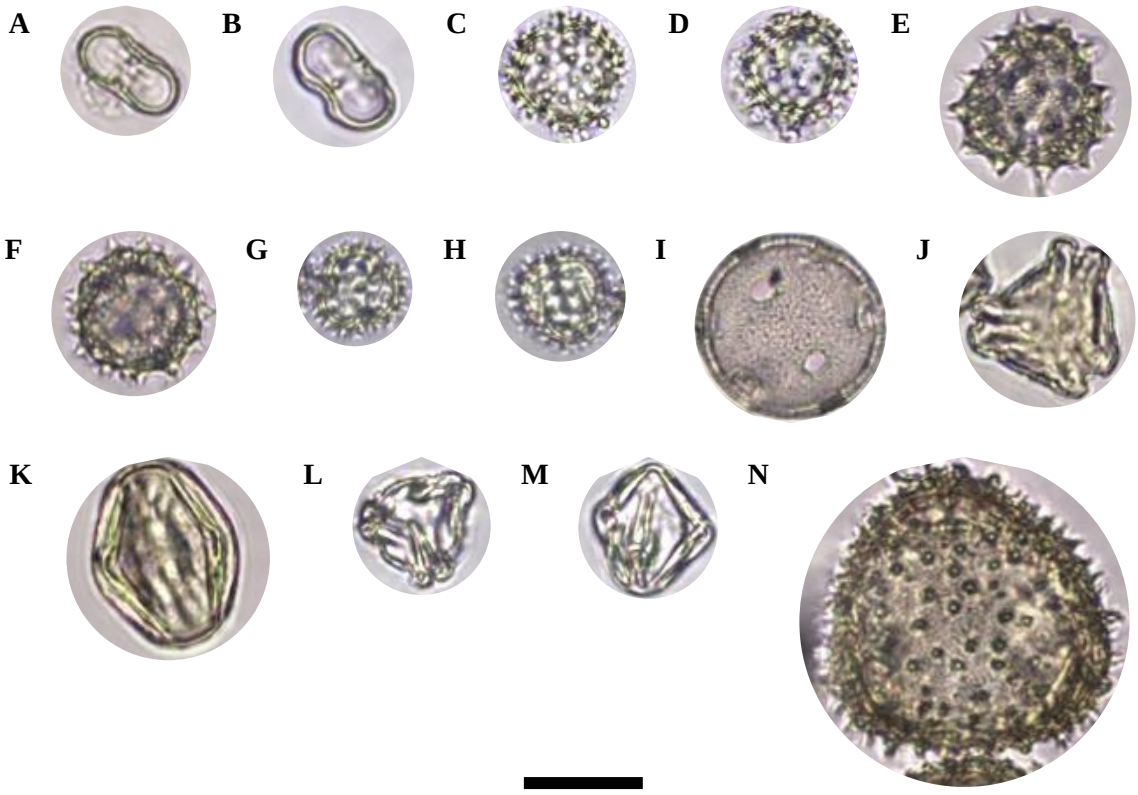


Figure 3 (continued)

Figure 3 (continued)

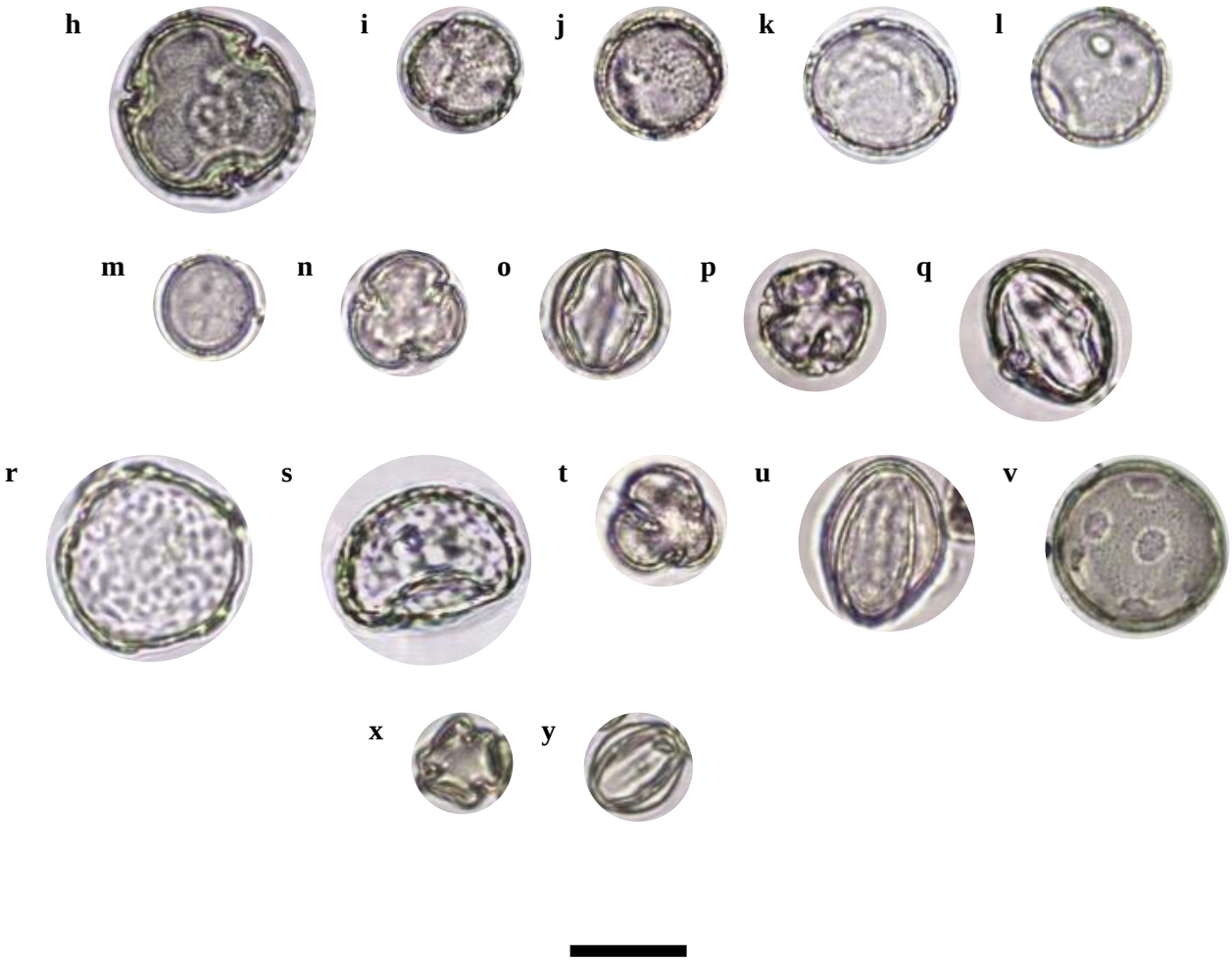
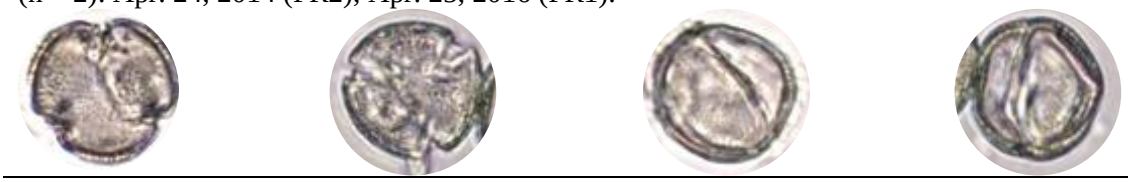


Figure 4. Description of morphotype specimens extracted from the frass of long-horned beetles. Qualitative characters ordered as pollen class (e.g., tricolporate, tricolpate), ornamentation (e.g., surface structures), and approximate shape (e.g., spheroidal, prolate, oblate; see Punt et al. 2007). Quantitative characters abbreviated: **E** = equatorial axis length, **P** = polar axis length, **P/E** = ratio of polar and equatorial axes, **PAI** = polar area index (e.g., quotient of the length between the colpi apices and polar axis length). Beetle collection information (e.g., species, number of beetles, collection date, study site) included. Beetle names abbreviated to first three letters of the genus and species. Floral host is included for beetles collected manually. Study sites corresponding to Table 1 as follows: **APR** = Allerton Park and Retreat Center, **FGP** = Forest Glen Preserve, **IFP** = Illinois Forestry Plantation, **NHW** = Nettie Hart Memorial Woods, **PR1** = Private residence #1 in Urbana, **PR2** = Private residence #2 in Urbana, **PR3** = Private residence #3 in Urbana, and **SAW** = South Arboretum Woods. Associate micrographs acquired under LED at 400 magnification, modified. Scale bar = 20 μm.

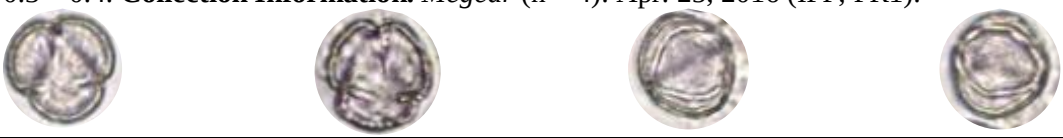
Type #1. Characters. Tricolporate, striate-reticulate, subprolate-prolate. E ≈ 20 μm; P ≈ 24 μm; P/E ≈ 1.2; PAI ≈ 0.2 – 0.4. **Collection Information.** *Cyrver* (n = 2): Apr. 18, 2016 (PR3) and Apr. 19, 2016 (NHW). *Megcar* (n = 1): Apr. 19, 2015 (PR1).

Type #2. Characters. Tricolpate, reticulate, spheroidal. E ≈ 24 μm; P ≈ 24 μm; P/E ≈ 1.0 – 1.2; PAI ≈ 0.5 – 0.7. **Collection Information**. *Calsan* (n = 1): Jun. 2, 2016 (NHW, *Cornus drummondii*). *Eudpin* (n = 2): Apr. 24, 2014 (PR2), Apr. 25, 2016 (PR1).



Type #3. Characters. Tricolpate, psilate, subprolate to prolate. E ≈ 11 μm; P ≈ 16 μm; P/E ≈ 1.45; PAI ≈ 0.6 – 0.8. **Collection Information.** *Elamuc* (n = 2): Aug. 12, 2015 (PR1), Aug. 17, 2015 (PR1).

Type #4. Characters. Tricolpate, striate, oblate to suboblate. E ≈ 20 μm; P ≈ 16 μm; P/E ≈ 0.8; PAI ≈ 0.3 – 0.4. **Collection Information.** *Megcar* (n = 4): Apr. 25, 2016 (IFP, PR1).



Type #5. Characters. Tricolporpate, scabrate to reticulate, suboblate to spheroidal. E ≈ 21 μm; P ≈ 19 μm; P/E ≈ 0.9; PAI ≈ 0.6 – 0.8. **Collection Information.** *Megcar* (n = 1): Apr. 24, 2016 (IFP).

Figure 4 (continued)

Type #6. Characters. Tricolporpate, reticulate, prolate to perprolate. E ≈ 20 µm; P ≈ 30 µm; P/E ≈ 1.5 – 1.75; PAI ≈ 0.3 – 0.6. **Collection Information.** *Eudpic* (n = 1): Jul. 6, 2015 (APR, *Daucus carota*). *Strsol* (n = 1): Jul. 2, 2015 (APR, *Daucus carota*). *Typvel* (n = 1): Jul. 6., 2015 (APR, *Daucus carota*).

Type #7. Characters. Tricolporpate, reticulate, subprolate to perprolate. E ≈ 18 – 20 µm; P ≈ 24 – 27 µm; P/E ≈ 1.4 – 1.8; PAI ≈ 0.2 – 0.3. **Collection Information.** *Analin* (n = 1): Jun. 8, 2016 (FGP, *Cornus drummondii*). *Calsan* (n = 3): Jun. 2, 2016 (NHW, *Cornus drummondii*), Jun. 8, 2016 (FGP, *Cornus drummondii*).

Type #8. Characters. Tricolporpate, scabrate, suboblate to spheroidal. E ≈ 24 µm; P ≈ 22 µm; P/E ≈ 0.9; PAI ≈ 0.3 – 0.5. **Collection Information.** *Cyrver* (n = 3): Apr. 18, 2015 (PR3), Apr. 18, 2016 (NHW).

Type #9. Characters. Tricolporate, faintly striate-reticulate, spheroidal to subprolate. E ≈ 18 µm; P ≈ 20 µm; P/E ≈ 1.1 – 1.2; PAI ≈ 0.3 – 0.5. **Collection Information.** *Molbim* (n = 4): Apr. 25, 2016 (SAW, *Cornus florida*).

Type #10. Characters. Tricolporate, striate, spheroidal to subprolate. E ≈ 18 µm; P ≈ 21 µm; P/E ≈ 1.0 - 1.1; PAI ≈ 0.3 - 0.6. **Collection Information.** *Megcar* (n = 4): Apr. 25, 2016 (PR1).

Figure 5. Shannon-Wiener Index (i.e., alpha diversity, evenness) for pollen grains from the frass of cerambycids collected from flowers. Bars with dark and light fill represent cerambycines and lepturines, respectively. **A)** Shannon-Wiener's Index for beetles collected on *Cornus drummondii* (Cornaceae) flowers. **B)** Shannon-Wiener Index for beetles collected on other flowers. Parenthetical letters are abbreviated names of floral hosts from which the beetles were collected: "Cm" = *Conium maculatum* (Apiaceae), "Dc" = *Daucus carota* (Apiaceae), "Cf" = *Cornus florida* (Cornaceae), "Sc" = *Solidago canadensis* (Asteraceae), and "Rm" = *Rosa multiflora* (Rosaceae).

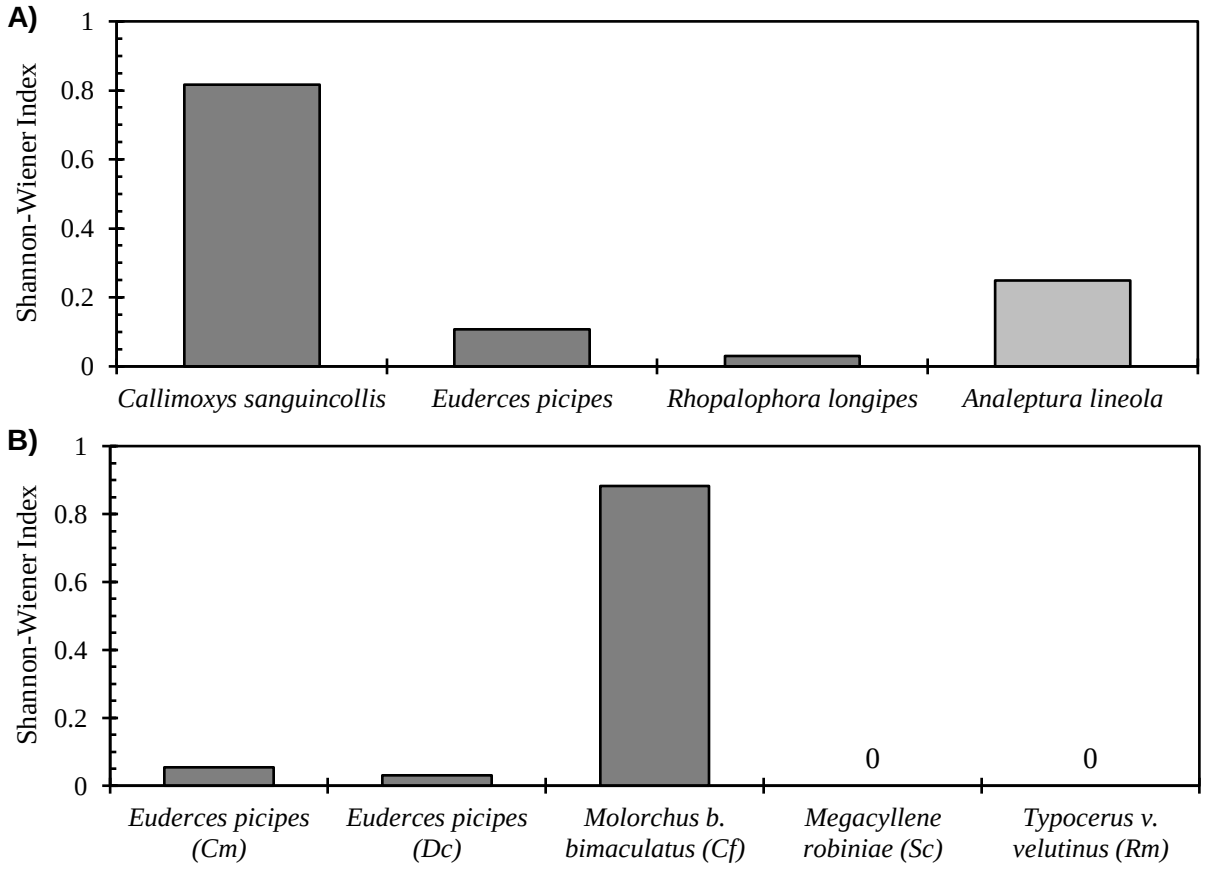
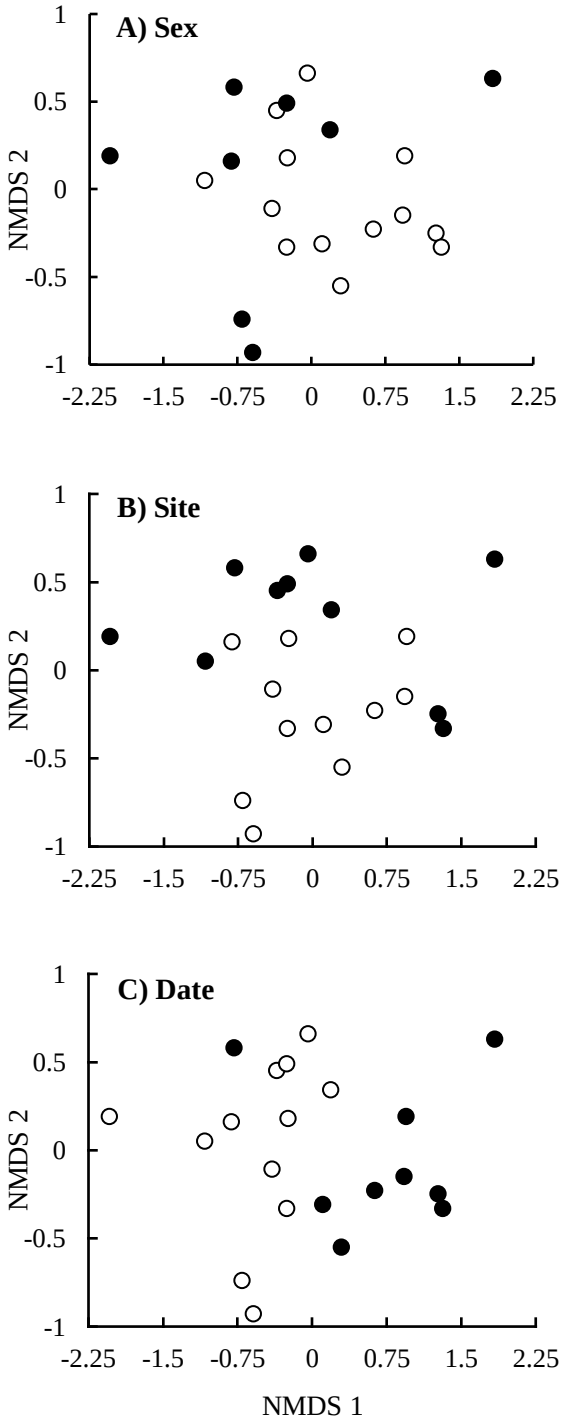


Figure 6. Four-dimensional nonmetric multidimensional scaling (NMDS) ordination of pollen composition recovered from *Megacyllene caryae* frass. Composition data were fourth-root transformed. Points represent frass samples from individual beetles. **A)** Filled circles (•) and unfilled circles (∘) signify male and female beetles, respectively. **B)** Filled and unfilled circles signify beetles collected at the IFP and PR1 sites, respectively. **C)** Filled and unfilled circles signify beetles collected on April 17, 2016 and April 24, 2016, respectively. Final 2D stress: 0.09.



APPENDIX A: REVIEW OF FLORAL HOST RECORDS

Floral hosts associated with the study the species reviewed from the literature. Floral host taxonomy and growth habit follows descriptions from the USDA-NRCS Plants database (2017). The growth form of the host is provided for species (and lower taxonomic classification) only: forbs or herbaceous (H), shrubs or subshrubs (S), trees (T), and vines (V). "X" signifies floral host association. Asterisks (*) and swords (†) signify anecdotal evidence (Dusham 1921) and palynivory observed in laboratory-reared specimens (Dusham 1921, Gosling 1984), respectively. Parentheses denote possible misclassifications (Lingafelter 2007). Literature reviewed: Dusham (1921), Knull (1947), Linsley (1963), Linsley and Chemsak (1976), Rice (1981), Gosling (1984b), Gosling (1986), Lago and Mann (1987), Berlocher et al. (1992), MacRae (1994), Yanega (1996), Schiefer (1998), Bond and Philips (1999), Lingafelter (2007), MacRae and Rice (2007), McDowell (2011), Hammond and Williams (2011), and Graham et al. (2012a).

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Apiales														
Apiaceae														
Cicuta maculata L.	H				X							X		X
Cryptotaenia canadensis (L.) DC.	H				X									
Daucus carota L.	H	X	X		X	X			X		X	X	X	X
Heracleum maximum Bartram	H	X	X		X				X			X	X	X
Osmorhiza caytonii (Michx.) C.B. Clarke	H											X		
Pastinaca sativa L.	H	X			X									

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Perideridia americana (Nutt. ex DC.) Rchb.	H				X									
Taenidia integerrima (L.) Drude	H										X			
Thaspium barbinode (Michx.) Nutt.	H										X			
Thaspium trifoliatum (L.) Gray	H				X									
Zizia aurea (L.) W.D.J. Koch	H				X									
Asterales														
Asteraceae														
Achillea millefolium L.	H													X
Carduus nutans L.	H												X	X
Cirsium arvense (L.) Scop.	H													X
Echinacea purpurea (L.) Moench	H													X

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Erigeron philadelphicus L.	H				X							X	X	X
Eupatorium perfoliatum L.	H													X
Eurybia divaricata (L.) G.L. Nesom	H													X
Grindelia Wild. sp.							(X)							
Leucanthemum vulgare Lam.	H				X								X	X
Parthenium integrifolium L.	H										X			
Rudbeckia hirta L.	H				X								X	
Solidago L. sp.							(X)							X
Solidago canadensis L.	H							X						
Solidago gigantean Aiton	H							X						
Solidago nemoralis Aiton	H							X						
Symphyotrichum lanceolatum ssp. *lanceolatum* var. *lanceolatum* (Willd.) G. L. Nesom	H							X						

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Symphyotrichum pilosum var. *pilosum* (Willd.) G. L. Nesom	H							X						
Campanulales														
Campanulaceae														
Campanulastrum americanum (L.) Small	H													X
Capparales														
Brassicaceae														
Hesperis matronalis L.	H											X		
Cornales														
Cornaceae														
Cornus L. sp.											X			
Cornus L. spp.						X								
Cornus alternifolia L.f.	T/S	X	X						X					
Cornus drummondii C.A.Mey.	T/S	X	X		X				X		X		X	
Cornus florida L.	T/S		X						X					

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Cornus foemina Mill.	T/S	X										X		
Cornus obliqua Raf.	S										X			
Cornus racemosa Lam.	S	X	X		X				X			X		
Cornus rugosa Lam.	T/S	X	X						X					
Cornus sericea L. ssp. *sericea*	T/S								X					
Dipsacales														
Caprifoliaceae														
Abelia R. Br. sp.											X			
Sambucus nigra L.	T/S				X									
Sambucus nigra L. ssp. *canadensis* (L.) R. Bolli	T/S				X									X
Sambucus racemosa L. var. *racemosa*	T/S								X					
Viburnum L. sp.		X							X					
Viburnum acerifolium L.	S		X		X				X			X		

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae									Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Viburnum dentatum L.	T/S	X							X					
Viburnum lentago L.	T/S		X											
Viburnum prunifolium L.	T/S													X
Viburnum rafinesqueanum Schult.	S	X												
Viburnum rufidulum Raf.	T/S								X					
Dipsacaceae														
Dipsacus fullonum L.	H													X
Euphorbiales														
Buxaceae														
Buxus L. sp.					X									
Euphorbiaceae														
Euphorbia corollata L.	H													X
Fabales														
Fabaceae														

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Cercis canadensis L.	T/S								X					
Melilotus officinalis (L.) Lam.	H													X
Mimosa nuttallii (DC. ex Britton & Rose) B.L. Turner	H													X
Orbexilum pedunculatum (Mill.) Rydb. var. *psoralioides* (Walter) Isely	H				X									
Trifolium pratense L.	H													X
Trifolium repens L.	H													X
Fagales														
Betulaceae														
Alnus Mill. sp.							X*							
Gentianales														
Apocynaceae														

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Apocynum androsaemifoliu L.	H													X
Apocynum cannabinum L.	H				X									
Asclepiadaceae														
Asclepias incarnata L.	H													X
Asclepias syriaca L.	H										X			X
Asclepias viridiflora Raf.	H				X									
Asclepias viridis Walter	H										X			
Geraniales														
Geraniaceae														
Geranium maculatum L.	H											X		
Lamiales														
Lamiaceae														
Monarda fistulosa L.	H													X

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Pycnanthemum tenuifolium Schrad.	H												X	X
Verbenaceae														
Callicarpa americana L.					X								X	X
Liliales														
Liliaceae														
Maianthemum racemosum (L.) Link ssp. *racemosum*	H											X		
Smilacaceae														
Smilax herbacea L.	H/V				X									
Magnoliales														
Magnoliaceae														
Liriodendron tulipifera L.	T										X			
Ranunculales														
Ranunculaceae														
Actaea racemosa L. var. *racemosa*	H													X

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Thalictrum dasycarpum Fisch. & Avé-Lall.	H	X	X						X					
Thalictrum pubescens Pursh	H													X
Rhamnales														
Rhamnaceae														
Ceanothus L. sp.		X									X			
Ceanothus americanus L.	S				X						X	X	X	X
Rosales														
Hydrangeaceae														
Hydrangea arborescens L.	S			X	X	X				X	X	X	X	X
Philadelphus coronarius L.	S				X									
Rosaceae														
Amelanchier arborea (Michx. f.) Fernald	T/S		X						X					

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae									Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Aronia x *prunifolia* (Marshall) Rehder	S								X					
Aruncus dioicus (Walter) Fernald var. *vulgaris* (Maxim) H. Hara	H				X				X			X		
Crataegus L. sp.			X				X[†]		X					
Crataegus chrysocarpa Ashe var. *chrysocapra*	T/S								X					
Crataegus crus-galli L.	T/S								X					
Crataegus mollis Scheele	T/S								X					
Crataegus viridis L.	T/S								X					
Geum canadense Jacq.	H				X									
Malus Mill. sp.									X					
Photinia x *fraseri* Dress											X			

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Physocarpus opulifolius (L.) Maxim. var. *intermedius* (Rydb.) B. L. Rob.	S				X				X					
Prunus L. sp.		X							X		X			
Prunus americana Marshall	T/S								X					
Prunus angustifolia Marshall	T/S								X					
Prunus umbellata Elliott	T/S					X								
Prunus serotina Ehrh.	T/S								X					
Prunus virginiana L.	T/S	X	X						X					
Pyrus L. sp.									X					
Rosa L. sp.											X			X
Rosa L. spp.													X	X
Rosa carolina L.	S				X								X	X
Rosa setigera Michx.	S/V				X								X	X
Rubus L. sp.					X						X	X		

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Sorbaria sorbifolia (L.) A. Braun	S													X
Sorbus aucuparia L.	T/S	X												
Spiraea sp.		X				X								
Spiraea x *vanhouttei* (Briot) Carrière.	S		X						X					
Spiraea alba Du Roi	S												X	X
Spiraea tomentosa L.	S													X
Rubiales														
Rubiaceae														
Cephalanthus occidentalis L.	T/S												X	X
Stenaria nigricans (Lam.) Terrell var. *nigricans*	H/S													X
Salicales														
Salicaceae														
Salix L. sp.									X					
Salix exigua Nutt.	T/S				X				X					

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Salix interior Rowlee	T/S				X							X	X	X
Salix nigra Marshall	T								X					
Sapindales														
Anacardiaceae														
Rhus glabra L.	T/S				X							X	X	X
Toxicodendron radicans (L.) Kuntze	H/S/V										X			
Rutaceae														
Ptelea trifoliata L.	T/S				X						X			
Sapindaceae														
Acer spicatum Lam.	T/S		X											
Staphyleaceae														
Staphylea trifolia L.	T/S								X					
Scrophularales														
Scrophulariaceae														
Verbascum thapsus L.	H													X

Appendix A (continued)

Floral Host Taxonomy	Growth Form	Cerambyincae										Lepturinae		
		Callimoxys sanguinicollis	*Cyrtophorus verrucosus*	*Elaphidion mucronatum*	*Euderces picipes*	*Euderces pini*	*Megacyllene caryae*	*Megacyllene robiniae*	*Molorchus b. bimaculatus*	*Neoclytus m. mucronatus*	*Rhopalophora lonipes*	*Analeptura lineola*	*Strangalia f. solitaria*	*Typocerus v. velutinus*
Solanales														
Convolvulaceae														
Ipomoea pandurate (L.) G. Mey.	H/V													X
Hydrophyllaceae														
Hydrophyllum appendiculatum Michx.	H											X		
Polemoniaceae														
Phlox L. sp.			X											
Phlox divaricata L.	H											X		
	TOTAL	**17**	**16**	**1**	**35**	**5**	**4**	**5**	**36**	**1**	**20**	**19**	**18**	**44**